

A mammalian fossil from the Dingqing Formation in the Lunpola Basin, northern Tibet, and its relevance to age and paleo-altimetry

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Received April 15, 2011; accepted July 26, 2011; published online September 27, 2011

The distal extremity of a rhinocerotid humerus from the upper part of the Dingqing Formation at the Lunbori locality in Baingoin County, northern Tibet, is the first mammalian fossil found in Cenozoic deposits of the Lunpola Basin. The medial condyle of the distal trochlea of the humerus specimen from Lunbori gradually contracts from medially to laterally. The margin of the medial surface of the medial condyle is not prominent, the well-developed medial epicondyle strongly extends posteriorly, and is divided from the articular facet of the medial condyle by a groove; all of which are characteristic for the Rhinocerotidae. The medial condyle is wide at the bottom and narrow at the top. The medial collateral ligament fossa is relatively shallow, and the medial collateral ligament tubercle is very weak. The medial part of the upper margin of the medial condyle smoothly connects to the bony surface above, but there is no clear boundary between them. All of these characteristics are identical with those of *Plesiaceratherium*. These comparisons imply that the Lunbori specimen is closest to *Plesiaceratherium gracile* in the Shanwang Fauna from Linqu, Shandong Province, in size and morphology. Thus, its age is suggested to be the late Early Miocene (Shanwangian Age), about 18–16 Ma. Discovery of the rhinocerotid fossil suggests that the upper part of the Dingqing Formation deposited in the Neogene. While adjusting to paleo-temperatures of the Early Miocene, a paleo-ecosystem reconstruction indicates that the paleo-elevation was close to 3000 m in the Lunpola Basin during this time.

Tibetan Plateau, Lunpola Basin, paleo-altimetry, Miocene, Dingqing Formation, Rhinocerotidae

Citation: Deng T, Wang S Q, Xie G P, et al. A mammalian fossil from the Dingqing Formation in the Lunpola Basin, northern Tibet, and its relevance to age and paleo-altimetry. Chin Sci Bull, 2012, 57: 261–269, doi: 10.1007/s11434-011-4773-8

The Rhinocerotidae is the family containing rhinoceroses whose characteristic feature is a chisel/tusk combination of the upper first incisor and the lower second incisor. The Rhinocerotidae reached their highest diversity in the Miocene, during which time they were widely distributed in Eurasia, North America, and Africa [1]. The rhinocerotids were herbivores, and most lived in tropical or temperate areas, but a few species, such as the woolly rhino (genus *Coelodonta*) lived in cold zones [2]. Rhinocerotid fossils are important standard fossils with strict chronological significance for the Cenozoic, and are important indicators of the

ecosystems inhabited by mammalian faunas.

The Lunpola Basin is located on the southern and northern sides of the boundary between Baingoin County and the Shuanghu Special District in northern Tibet. The basin has well-developed Cenozoic strata and an average elevation of about 4700 m a.s.l. The total thickness of Cenozoic deposits in the Lunpola Basin is over 4000 m, and consists of the Niubao Formation in the lower part and the Dingqing Formation in the upper part. The Tertiary age of these deposits is not in question, but there have been different opinions about their ages at the epoch or series levels [3–6]. Previously, the lack of mammalian fossils strictly constrained the subdivision and correlation of these Cenozoic strata. The

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paleontological evidence to identify ages in this basin has depended mainly on sporopollens and ostracods. Estimations of the paleo-elevation of the Lunpola Basin have been very different using these datasets. During the deposition of the Dingqing Formation, the lowest estimate has been reported to be about 1000 m [7], but the highest published estimate is 4500 m [8]. Guided by previous reports [9], in 2009 and 2010, we carried out an extensive and detailed investigation of the stratigraphy and a survey for vertebrate fossils. We found more beds and specimens of fish fossils in the Dingqing Formation. Most importantly, we found a rhinocerotid fossil in the Dingqing Formation, which is significant for age determination and the paleo-altimetry estimation. In this paper, we present and discuss our study of this mammalian fossil from the Lunpola Basin.

1 Geological setting

The Lunpola Basin is a Cenozoic terrestrial basin, which developed on Yanshanian folded basement rocks. Its formation and evolution are related to the movement history of the Bangong-Nujiang deep fault. Relative right-lateral wrench movement of this fault caused production of the NNE-SSW oriented tensile stress in this area, where a strike-slip extensional basin was formed [10].

The Lunpola Basin is elongated, beginning in the east near Dongqiao and ending at Duojialing to the north of Siling Co (lake) in the west. It has an E-W length of about 200 km, a N-S width of about 15–20 km, and an area of over 4000 km². The names of the Dingqing and Niubao formations are derived from the Dingqing and Niubao beds that were nominated by the Qinghai Petroleum Survey Team in 1957. The Dingqing Formation is widely distributed in the central and eastern parts of the Lunpola Basin, and consists of a series of greenish-gray mudstones and shale alternating beds of sandstones and oil shales, with a thickness of 300–1100 m. It bears rich animal and plant fossils, such as ostracods, gastropods, insects, fishes, and sporopollens. The Niubao Formation is distributed throughout the entire basin. It is a series of red clastic rocks alternating beds of grayish-green mudstones and sandstones, with a thickness of 700–950 m, bearing comparatively fewer fossils, including ostracods, sporopollens, and charophytes [6].

The Tertiary deposits of the Lunpola Basin were first discovered and confirmed in 1955 [11], and were subdivided into three beds. In 1975, the strata of the Lunpola Basin were first subdivided based on fossils into four formations, the Diou, Niubao, Dingqing, and Lunpola formations of the Eocene, Oligocene, Miocene, and Pliocene, respectively [3]. In 1982, based on ostracod fossils, the Niubao Formation was referred to the Eocene, the Dingqing Formation was referred to the Oligocene, the Diou Formation was included in the Niubao Formation, and the Lunpola Formation was

included in the Dingqing Formation [4]. In 1983, the upper member of the Dingqing Formation was referred to the Pliocene, the middle member to the Miocene, and the lower member to the Late Oligocene, and the Niubao Formation was referred to the Eocene-Oligocene [6]. Recently completed geological mapping of the Tibetan Plateau indicates that the Niubao Formation has four ostracod assemblages from its base to top. These are the *Limnocythere-Eucypris*, *Limnocythere-Cypris-Cyprinotus*, *Limnocythere-Cypris-Eucypris-Candona*, and *Cypinotus-Candona* assemblages from the Eocene [12]. The Dingqing Formation has two ostracod assemblages from its base to top, the *Austrocypris-Cyprinotus-Pelocypris* and *Ilyocypris-Limnocythere* assemblages [13] from the Oligocene [14].

The Lunbori area is located in the center of Lunpola Basin (Figure 1) and tectonically belongs to the Nakaco-Dongkaco central landmass. This tectonic unit is a rigid landmass that is situated between the southern and northern zones of the Bangong-Nujiang suture, which consists mainly of the Mesozoic Jurassic Jienu Group and Early Cretaceous Qushenla Formation, overlain by the Dingqing Formation.

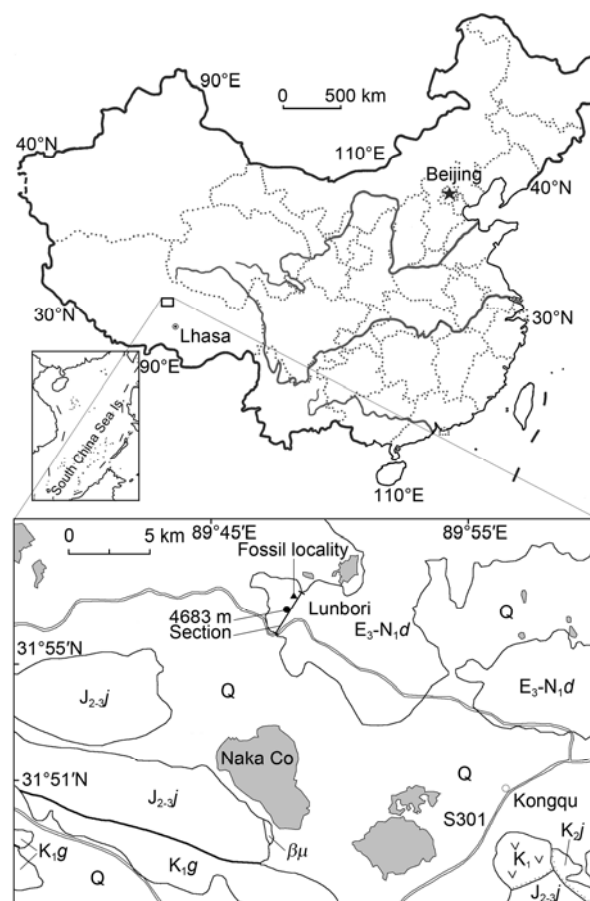


Figure 1 Geological map and location of the fossil site around Lunbori in the Lunpola Basin. K_{2j}, Upper Cretaceous Jingzhushan Fm.; J_{2-3j}, Middle-Upper Jurassic Jienu Group; K₁, Lower Cretaceous volcanic rock; K_{1g}, Lower Cretaceous Guiya Fm.; E₃-N_{1d}, Oligocene-Miocene Dingqing Fm.; Q, Quaternary; βμ, diabase dike. Modified from [12].

The tectonics in this area are dominated by faults that developed parallel to the southern zone of the Bangong-Nujiang suture, superimposed multiple times with a successive activation, and expressed mainly as clockwise right-lateral shearing [12].

In this study, the total thickness of the section of the Dingqing Formation at Lunbori is 989.5 m. Layers 1–4 alternated between gray thick- to huge thick-bedded shale and thin-bedded limestones, banded gray oily shale, brownish yellow shale, and light brown silty marlites, with rich plant and insect fossils in the middle part and a thickness of 109.4 m. Layers 5–9 alternated between gray shale and brownish-gray paper-thin oil shale, containing well-preserved fish, insect, and plant fossils, as well as horizons of banded brownish-yellow thin-bedded siderites, with a thickness of 583.7 m. Layers 10–18 alternated between brownish-gray thickly bedded paper-thin oil shale and thickly bedded gray shale, banded reddish-brown, gray, and light yellow massive mudstones bearing bivalve, fish, and mammal fossils in the upper part, and brown thin-bedded silty mudstones and thin-bedded tuffaceous sandstones with a thickness of 209.3 m. Layers 19–28 constituted gray thin-bedded mudstones, marlite, and gray thin-bedded shale, banded brownish-grey paper-thin oil shale and light yellow thin-bedded marlites with a thickness of 87.1 m (Figure 2). The mammalian fossil reported in this paper was collected from the reddish massive mudstones of layer 17, which comprises the distal extremity of the left humerus of a rhinocerotid. This fossil locality is situated on the northern side of Lunbori Hill (Figure 3), with geographic coordinates of 31°57'27.6"N and 89°47'55.7"E, and an elevation of 4624 m. There is also a great number of scattered fish bone fossils and many bivalve fossils at this location.

2 Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Owen, 1845

Subfamily Aceratheriinae Dollo, 1885

Genus *Plesiaceratherium* Young, 1937

Plesiaceratherium sp.

(i) Material. The medial part of the distal extremity of a left humerus with the complete medial condyle and the residual epicondyle (Figure 4(a)), IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) catalogue number V 18082. This specimen is strongly lithified. It is yellowish brown, with black spots on the surface, and a black film could be seen in the broken section. Due to corrosion from plant alkaloids in grass roots, white root prints were evident on the partial surface, which are similar to those in preserved mammalian fossils from the Bulong Basin in Biru County, Tibet [15].

(ii) Description. The medial condyle of the distal trochlea

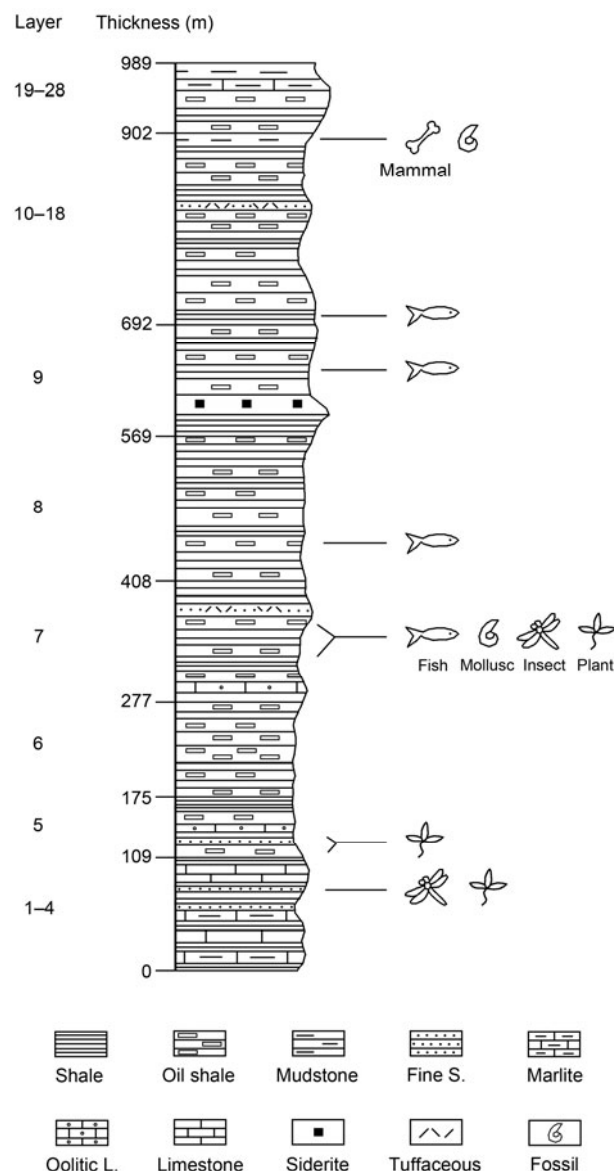


Figure 2 Columnar section at Lunbori in the Lunpola Basin. S, sandstone; L, limestone.

of the humerus is a cone that is gradually constricted medially to laterally. Its articular surface lacks a secondary separation, which articulates with the glenoid fossa of the radius and the semilunar notch of the ulna (Figure 4(a3)). In anterior view, the medial condyle is wide at the lower end and narrow at top, so that its upper part is inclined to the midline of the shaft. The medial part of the upper margin of the medial condyle is smoothly connected to the bony surface above and lacks a prominent edge (Figure 4(a2)). In medial view, the residual part of the epicondyle implies that it is well-developed. The lower margin of the epicondyle is clearly higher than the medial surface of the medial condyle, and the anterior end of the former penetrates into the lower part of the latter. Thus, the connection between the anterior end of the medial epicondyle and the posterior end of the



Figure 3 Lunbori fossil locality in the Lunpola Basin.

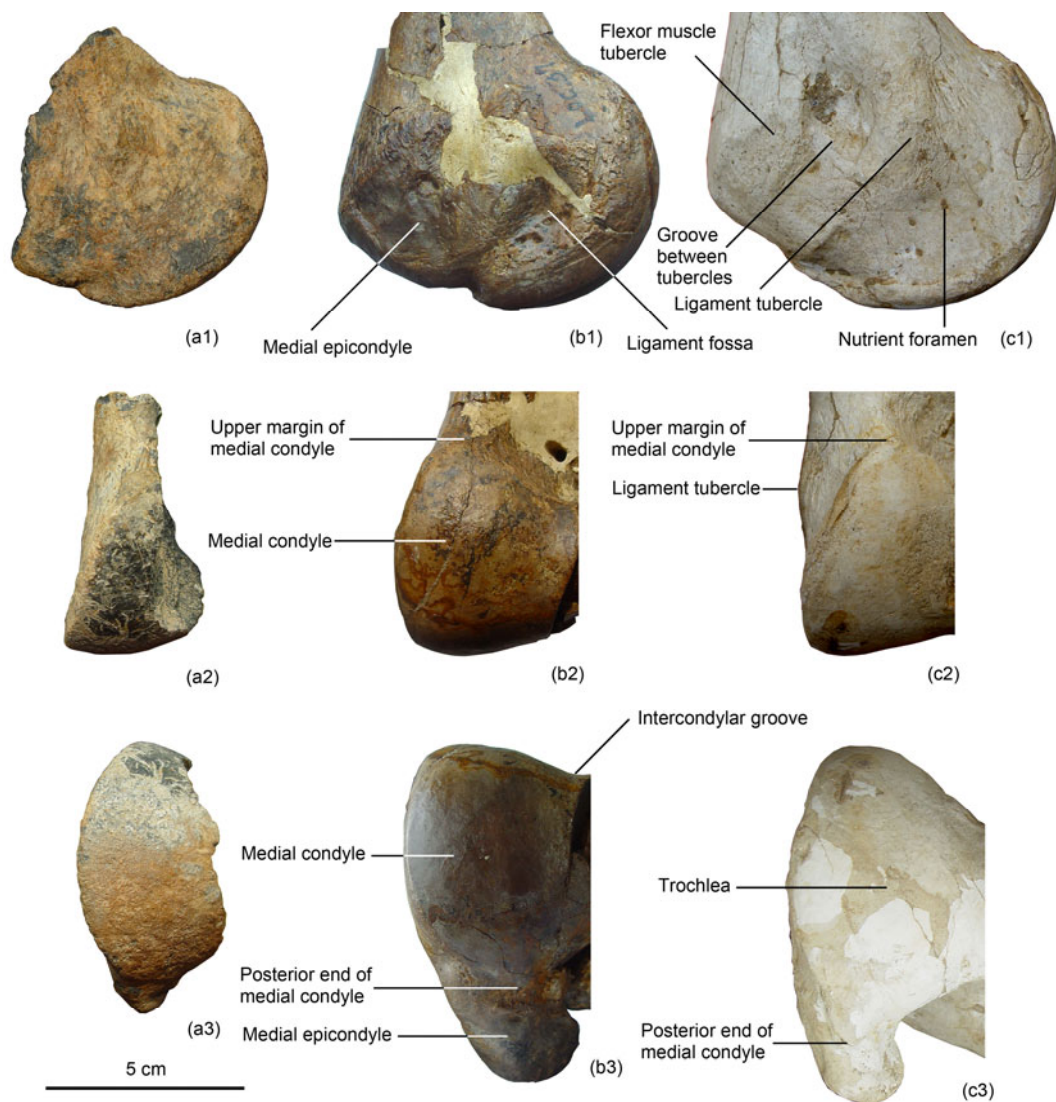


Figure 4 Comparison between the Lunbori specimen and the distal extremities of the humeri of *Plesiaceratherium gracile* and *Chilotherium wimani*. a, *Plesiaceratherium* sp., V 18082 from Lunbori, Baingoin, Tibet; b, *Plesiaceratherium gracile*, RV 37065 from Shanwang, Linqu, Shandong; c, *Chilotherium wimani*, H MV 0449 from Houshan, Guanghe, Gansu Province. 1, Medial view; 2, anterior view; 3, distal view.

medial condyle forms a nearly horizontal groove. The marginal area of the medial surface of the medial condyle is a rough crescent with a width of 7 mm at the middle, the two

ends of which disappear at the upper and lower ends of the medial condyle. There are some minute rounded pits on the middle and lower parts of the medial surface of the medial

condyle, which are the openings of the nutrient foramina with a maximum diameter of 1 mm. The medial collateral ligament fossa is relatively shallow, with an unclear border and a gradual transition to the bony surface. In this fossa, there is a fine crest oblique from anterosuperior to postero-inferior, with a length of 12 mm, which coincides with the connecting line between the upper and lower ends of the medial condyle. The center of the medial collateral ligament fossa is situated at the midpoint of this line. The medial collateral ligament tubercle is weakly prominent and located above the collateral ligament fossa, also with a central fine crest parallel to the crest in the fossa and equal to the length of the latter. Behind the collateral ligament tubercle is a vertical, wide, and shallow depression, which separates the collateral ligament tubercle from another tubercle attached to the superficial digital flexor muscle on the medial surface of the medial epicondyle (Figure 4(a1)). In distal view, the medial condyle does not extend posteriorly, and its posterior end does not reach the anteroposterior midline of the medial epicondyle (Figure 4(a3)). The maximum diameter of the medial condyle is 67.5 mm.

(iii) Comparison. The Lunbori specimen is different from artiodactyl humeri. In an artiodactyl humerus, the central part of the medial condyle of the distal trochlea is not lower than the medial part so that the medial condyle is not constricted or only weakly constricted, and even slightly expanded from medially to laterally. For example, in bovids, the central diameter of the medial condyle of the distal trochlea is larger than the medial one [16].

In perissodactyl humeri, the medial condyle of the distal trochlea in horses has the same anteroposterior diameter or is only slightly enlarged from medially to laterally, but abruptly becomes small near the intercondylar groove, and is crossed by a sagittal groove [17]. In tapirs, the medial surface of the medial condyle is convex as a whole, and the medial epicondyle is strongly developed and is transversely very thick, with an anteroposterior length close to that of the medial condyle. In chalicotheres, the medial condyle has an asymmetric constriction from medially to laterally, the anterior part of the medial margin has a small articular facet. The medial epicondyle is transversely wide, but anteroposteriorly short [18,19]. In titanotheres, the lower margin of the medial epicondyle strongly rises, with a relatively large distance from the lower margin of the medial condyle, although the anterior part of the medial margin of the medial condyle in some titanotheres forms is distinctly concave [20,21]. In the humeri of rhinoceroses, the medial condyle of the distal trochlea is a comparatively symmetric cone constricted gradually from medially to laterally, and lacks a sagittal groove or ridge to subdivide it [16]. The morphologic features of the Lunbori specimen are identical to those of rhinoceroses.

The Rhinoceroidea is a group of perissodactyls with the highest diversity of species and habitats and is generally divided into three families (i.e. Hyracodontidae, Amyno-

dontidae, and Rhinocerotidae [22]).

In *Imequincisoria* sp. [23], for example, the margin of the medial surface of the medial condyle of the distal trochlea forms a wide crescent ridge for the hyracodont's humerus. The medial epicondyle weakly extends posteriorly and inferiorly. The medial surface is very uneven. The medial collateral ligament fossa and tubercle are marked and located above the connecting line between the upper and lower ends of the medial condyle. The lower margin of the medial epicondyle has a continuous transition to the lower margin of the medial condyle, without a distinct boundary between them in medial view. The depression between the medial collateral ligament tubercle and the superficial digital flexor muscle tubercle is relatively large. The giant rhinos, which were included in the Hyracodontidae, have the same features, such as the humerus of *Juxia sharamurenensis* [24].

In *Gigantamynodon promises* [25], for example, the medial epicondyle of the distal extremity for the amynodont's humerus is less developed and steeply inclined posterosuperiorly, and its lower margin has a gradual transition to the lower margin of the medial condyle in medial view. The small and deep collateral ligament fossa is tightly situated under the highly raised collateral ligament tubercle that is a triangular pyramid, and the former is located at the connecting line between the upper and lower ends of the medial condyle. The crescent ridge on the medial surface of the medial condyle is strongly prominent. The tubercle that is attached to the superficial digital flexor muscle is a prominent crest that extends to the posterior margin of the medial surface.

In the humeri of the Rhinocerotidae, the margin of the medial surface of the medial condyle is not prominent and the medial epicondyle is well developed and strongly extends posteriorly with a groove to divide it from the articular surface of the medial condyle. Clearly, the Lunbori specimen belongs to the Rhinocerotidae. Comparing with different taxa within the Rhinocerotidae, the Lunbori specimen is almost identical to the distal extremity of the humerus of *Plesiaceratherium gracile* (Figure 4(b)) from the late Early Miocene Shanwang Fauna from Linqu County, Shandong Province. The above-mentioned features of the distal extremity of the Lunbori humerus can be seen in the specimen IVPP RV 37065 of *P. gracile*. In *P. gracile*, for example, the upper part of the medial condyle is inclined to the midline of the shaft, and its upper margin is smoothly connected to the bony surface. The lower margin of the epicondyle is clearly higher than the medial surface of the medial condyle, and the anterior end of the former penetrates into the lower part of the latter, so that their connection forms a nearly horizontal groove. On the medial surface of the medial condyle, the crescent surface is marked, and the nutrient foramina are rich. The medial collateral ligament fossa has no a clear border, and the collateral ligament tubercle is weakly prominent. The depression is wide and shallow

between the collateral ligament and the superficial digital flexor muscle tubercles. The medial condyle does not extend posteriorly. For the humerus (IVPP RV 37065) of *P. gracile*, the maximum diameter of the medial condyle is 67 mm, which is also close to that of the Lunbori specimen (67.5 mm). Minor differences are the more marked collateral ligament fossa and the smoother medial surface of the medial condyle in *P. gracile* (Figure 4(b1)) than in the Lunbori specimen. Thus, we identified the Lunbori specimen as *Plesiaceratherium* sp.

Within the Rhinocerotidae, many medium-sized forms are similar to the Lunbori specimen in size, but different in morphology. In the humerus of *Chilotherium wimani*, for example, the lower margin of the medial epicondyle of the distal extremity is strongly inclined posterosuperiorly, and the anterior margin does not reach the posterior part of the medial condyle of the trochlea in medial view. There is no notch or groove between the epicondyle and the condyle. The collateral ligament tubercle is relatively prominent, but the collateral ligament fossa is very weak (Figure 4(c1)). In anterior view, the upper margin of the medial condyle is clearly higher than the bony surface, forming a projecting edge (Figure 4(c2)). In distal view, the medial condyle strongly extends posteriorly, the posterior end of which greatly exceeds the anteroposterior midline of the medial epicondyle (Figure 4(c3)) [26].

In the woolly rhinos (genus *Coelodonta*), which were capable of living in alpine and cold zones, the distal extremity of the humerus is quite different to that of the Lunbori specimen. First, their sizes differ greatly, the diameter of the medial condyle of the distal trochlea is 98 mm in the smaller *C. nihowanensis* [27], and 119 mm in the Late Pleistocene *C. antiquitatis* [28], both of which are much larger than the Lunbori specimen, which is 67.5 mm. Second, with regards to morphology, the collateral ligament fossa is indistinct on the medial surface of the distal extremity of the woolly rhino's humerus, but the collateral ligament and superficial digital flexor muscle tubercles are well developed, both of which are close to and even fused to each other. The lower margin of the medial epicondyle is much higher than that of the medial condyle, between which there is a distance of about 20 mm [28,29].

3 Discussion of age

Plesiaceratherium was established as a genus based on some isolated teeth and limb bones found in Early Miocene strata at Shanwang in Linqu, Shandong Province, with *P. gracile* serving as the type species [30]. Later, additional materials of *Plesiaceratherium* were discovered from Shanwang, including many well preserved skeletons, complete skulls, and many teeth and limb bones, which allowed detailed observations of the characteristics of *Plesiaceratherium* [31,32]. *Plesiaceratherium* is a medium- to large-sized

primitive acerathere rhinoceros with slender limb bones. Previously, *Plesiaceratherium* was found only in two localities in China, i.e. Shanwang in Linqu, Shandong Province, and Jiulongkou in Cixian, Hebei Province [33]. In addition, *Plesiaceratherium* is distributed in Europe at five localities, Sandelzhausen (MN 5) and Voggersberg (MN 5) in Germany, Pont du Manne (MN 4) in France, Charneca de Lumiar (MN 4) in Portugal, and Can Julia (MN 4) in Spain [1].

The Chinese Shanwang and Jiulongkou faunas bearing *Plesiaceratherium* were determined to be from the late Early Miocene Shanwangian Age, and the European fossil localities bearing *Plesiaceratherium* belong to MN 4–5 in the late Early Miocene Orleanian Age [1], which corresponds to the age of *Plesiaceratherium* in China.

Since the Mesozoic and Cenozoic strata in the Linqu Depression, in which the Shanwang area is located, are a series of volcanic and sedimentary rocks, radiometric dating has been well established for this basin. The published data, which are relatively consistent with the age of the fossils, indicate that a diatomite with rich fossils has been reported to be deposited between 18.85 and 14.11 Ma [34], or 18.05 ± 0.55 Ma [35]. In addition, because the samples were collected beneath the Shanwang Formation, the age of the Shanwang Fauna was about 18 Ma [36]. The fossil locality of the Jiulongkou Fauna cannot be dated radiometrically, the locality includes several members of the Shanwang Fauna, such as *Plesiaceratherium* and *Palaeomeryx*, and also the younger *Percrocuta* [33]. Thus, its period should be the latest Shanwangian Age at about 16 Ma. The five localities bearing *Plesiaceratherium* in Europe belong to MN 4 or 5 of the mammalian ages at 18–15 Ma [37]. In conclusion, the localities in *Plesiaceratherium*'s distribution in Eurasia are very close in age, i.e. the late Early Miocene.

Based on the *Plesiaceratherium* fossil found at the Lunbori locality in the Lunpola Basin, the upper part of the Dingqing Formation was deposited in the Miocene. Originally, and in general terms, the ostracod fossils of the Dingqing Formation were considered to be of Oligocene age [4,13,14]. However, the fossils from different layers or members should have different ages. The upper part of the Dingqing Formation, which is near the *Plesiaceratherium* layer, yield the ostracods *Heterocypris formalis*, *Heterocypris subsinuatus*, *Candoniella albicans*, *Ilyocypris errabundis*, *Ilyocypris dunschanensis*, and *Limnocythere cinctura* [4,38]. Among them, *L. cinctura* was found from the Yancheng Formation in Jiangsu Province [39], with an age corresponding to that of the Early Miocene Shanwang Formation [40]; *I. dunschanensis* appeared only in the Neogene. *C. albicans* and *I. errabundis* were distributed from the Paleogene to the Neogene [38]. A comprehensive correlation indicates that the ostracod assemblage in the upper part of the Dingqing Formation is characteristic of the Early Miocene. Because the lower part of the Dingqing Formation preserves extensive thick-beds of oil shale and fine clastic deposits, new evidence combined with the ostracod fossils,

supports the opinion that the entire Dingqing Formation belongs to the Oligocene and Miocene [6].

4 Estimation of paleo-altimetry

The fossils of *P. gracile* appear in great numbers in the Shanwang Fauna in Linqu, Shandong Province. This species, together with *Palaeomeryx tricornis* and *Lagomeryx colberti*, are dominant forms with respect to individual numbers in the fauna. In addition to rich mammalian fossils, the Shanwang locality also produced fossils of fishes, amphibians, reptiles, birds, insects, large plants, sporopollens, and algae. Thus, the habitat of *Plesiaceratherium* can be reconstructed rather accurately. The mammals from Shanwang are mainly forms that lived on the forest edge and in swampy areas, especially *P. tricornis*, *L. colberti*, and various squirrels (*Tamiops asiaticus*, *Sciurus lii*, *Oriensciurus linquensis*, and *Plesiosciurus* aff. *sinensis*) [41]. However, forms that lived in grasslands are rare, which indicates that the ecosystem was a subtropical or warm temperate forest during that time. Judging from the flora in Shanwang Basin, many species are subtropical evergreen or deciduous broad-leaved plants, which also indicate a warm and humid climate [31,42]. The central area of Shandong Peninsula, where Shanwang of Linqu is located, has an elevation of less than 1000 m, and the ecosystems of the Shanwang Fauna imply that the elevation during the Early Miocene was similar to the modern one. The distribution of *Plesiaceratherium* in Europe also was at a lower elevation (<1000 m), where the Early Miocene ecosystem flourished in a warm and humid climate between 18–16.5 Ma [43]. Thus, we can conclude that *Plesiaceratherium* was a rhinoceros that preferred warm and humid conditions and lived in subtropical or warm temperate forests.

A detailed sporopollen analysis of the Dingqing Formation [3] showed that the lower part had an *Ulmus-Salix* assemblage. We also recently found leaf fossils of *Salix* in the Dingqing Formation, which is consistent with sporopollen data. In the middle part, angiosperm pollen was more plentiful than gymnosperm pollen, accounting for 55%–73% of the total amount. Thus, angiosperm plants were abundant, dominated by northern temperate deciduous broad-leaf trees, among which *Quercus*, *Salix*, and *Juglans* were the most common. They were the main tree species of that time. The conifers primarily included *Pinus*, *Picea*, and *Abies*, which were secondary forest components. Herbaceous plants began to further develop. In the upper part, angiosperm pollen dominated the assemblage, accounting for 88%–91%, and gymnosperm pollen was less abundant. *Salix* pollen rapidly increased, becoming the dominant species along with *Quercus* in this assemblage, and *Rhus* pollen also was abundant. Other woody plants included *Juglans*, *Betula*, *Celtis*, *Magnolia*, *Acer*, *Corylus*, *Carya*, and *Pterocarya*. The sporopollen assemblage of the Dingqing For-

mation is similar to that of the Shanwang Formation in Linqu, Shandong Province, reflecting the warm and humid climate at that time [3]. The melanic deposits are well developed in the Dingqing Formation, which indicates a humid climate or environment during that time [44,45]. In summary, the rhino *Plesiaceratherium* lived in a warm and humid habitat similar to those in Shandong Province and Western Europe during the Early Miocene.

As mentioned above, paleo-altimetry estimates for the Lunpola Basin during the time of deposition of the Dingqing Formation are very different, ranging from about 1000 m [7] to 4500 m [8]. Based on a direct comparison, elevations of the distribution of *Plesiaceratherium* in Shandong Province and Western Europe support a paleo-altimetry estimation of about 1000 m in the Lunpola Basin during that time. However, a more reasonable estimate must be determined for the highest limit of subtropical or warm temperate forests given the global climatic and environmental conditions during the Early Miocene.

The distribution of animals and plants on the southern slope of the Himalaya Mountains along the southern border of the Tibetan Plateau has distinct vertical zones. In this area, the upper limit of the evergreen broad-leaf forest is 2500 m a.s.l. with a warm and humid climate, an annual rainfall of about 2000 mm, and varied taxa of animals with large populations [46]. Based on animal and plant characteristics, the habitat of the Shanwang Fauna bearing *Plesiaceratherium* and the Lunpola *Plesiaceratherium* were similar to this kind of evergreen broad-leaf forest.

Given this global climatic background, the rhino *Plesiaceratherium* lived between the two cooling events of Mi-1b at 17.8 Ma and Mi-2 at 16 Ma [47], but the temperature during that time was higher than that of the modern levels [48]. In fact, the historic temperature was 4°C higher than modern temperatures (calculated from oxygen isotopes [49]). The distribution of vertical vegetation zones is directly related to atmospheric temperature, with a temperature lapse rate of 0.6°C/100 m [50]. As a result, a temperature increase of 4°C would drive the boundaries of the vertical vegetation zones about 670 m higher. Thus, during the Early Miocene, the evergreen broad-leaf forest that was suitable for *Plesiaceratherium* would have been at a maximum elevation of 3170 m.

In modern times, species of the Rhinocerotidae are still distributed in South Asia on the south side of the Tibetan Plateau, including Nepal where the Indian rhino (*Rhinoceros unicornis*) lives in forest and grassland areas at the foot of the Himalayas. Among extant rhinoceroses, the Sumatran rhino (*Dicerorhinus sumatrensis*) can live in tropical rain forests at elevations of 1000–1500 m because of its hairy coat [51]. The highest distribution of the Javan rhino (*Rhinoceros sondaicus*) was recorded at 2000 m a.s.l. [52]. Given this optimum ecological range for the extant rhinoceroses, and through an elevation adjustment of 670 m derived by a temperature lapse rate [50] of 4°C higher in the

Early Miocene [49], the maximum paleo-altimetry of *Plesiaceratherium*'s habitat during the Early Miocene in the Lunpola Basin should be close to 3000 m a.s.l.

5 Conclusions

The age of Cenozoic deposits in the Lunpola Basin in northern Tibet has been disputed for a many years, primarily because of a lack of fossils with accurate chronological significance. The distal extremity of a rhinocerotid humerus from the upper part of the Dingqing Formation at the Lunbori locality in Baingoin County is the first mammalian fossil found in the Cenozoic deposits of the Lunpola Basin. Our detailed observations and comparisons show that its medial condyle is wide at the bottom and narrow at the top, the medial collateral ligament fossa is relatively shallow, and the medial collateral ligament tubercle is very weak. The medial part of the upper margin of the medial condyle smoothly connects to the bony surface above, but lacks a clear boundary between them, which indicates that this specimen was *Plesiaceratherium* sp. of the Rhinocerotidae.

Plesiaceratherium has previously been found in eastern China and Western Europe, and the strata bearing this rhino's fossils in the two regions have been correlated to the late Early Miocene. Radiometric dating for the Shanwang Basin in Linqu County, Shandong Province indicates that *Plesiaceratherium* lived between 18–16 Ma. Thus, the upper part of the Dingqing Formation bearing the *Plesiaceratherium* fossil was deposited during the late Early Miocene, and the entire Dingqing Formation included Oligocene–Miocene deposits.

The vegetation type of the Dingqing Formation was identical to that of the Shanwang Fauna and *Plesiaceratherium* has been inferred to live in subtropical and warm temperate forests, preferring a warm and humid climate. The correlations and adjustments based on modern alpine vegetation vertical zones in the Himalayas and the Early Miocene global climatic conditions indicate that the highest elevation in the Lunpola Basin at the time of the deposition of the Dingqing Formation could not have exceeded 3170 m a.s.l. Thus, considering the ecological requirements of rhinoceroses through a paleo-temperature adjustment for the Early Miocene, the most reasonable paleo-elevation for *Plesiaceratherium* is close to 3000 m a.s.l.

We appreciate the support and cooperation of Prof. Ding Lin of the Institute of Tibetan Plateau Research, Chinese Academy of Sciences (CAS), Prof. Sun Jimin and Prof. Liu Qingsong of the Institute of Geology and Geophysics, CAS, and Dr. Zhao Min, Dr. Wu Feixiang, Dr. Wang Ning, Mr. Shi Fuqiao, and Wu Shengli of the Institute of Vertebrate Paleontology and Paleoanthropology, CAS, for their assistance during field work. We are also grateful for constructive comments from the reviewers of this manuscript. This work was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-Q09), the National Basic Research Program of China (2012CB821906), and the National Natural Science Foundation of China (40730210).

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